Prey speed influences the speed and structure of the raptorial strike of a 'sit-and-wait' predator

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Prey speed influences the speed and structure of the raptorial strike of a 'sit-and-wait' predator

Sergio Rossoni[1,2] and Jeremy E. Niven[1]

[1] School of Life Sciences, University of Sussex, Falmer, Brighton, BN1 9QG, United Kingdom
[2] Current address: Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, United Kingdom

Author for correspondence:
Sergio Rossoni or Jeremy E. Niven
e-mail: sr779@cam.ac.uk or j.e.niven@sussex.ac.uk

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Predators must often employ flexible strategies to capture prey. Particular attention has been given to the strategies of visual predators that actively pursue their prey, but sit-and-wait predators have been largely overlooked, their strategies often characterised as stereotyped. Praying mantids are primarily sit-and-wait predators that often employ crypsis to catch their prey using a raptorial strike produced by their highly modified forelimbs. Here we show that the raptorial strike of the Madagascan marbled mantis (*Polyspilota aeruginosa*) varies in duration from 60 to 290 ms due to the tibial extension alone; slower strikes involve slower tibial extensions that may also be interrupted by a pause. The success of a strike is independent of its duration or the presence of these pauses. However, prey speed affects the duration of tibial extension and the probability of a pause occurring, both increasing at slower prey speeds. Adjusting the duration of the tibial extension according to prey speed allows mantids to time the final downward sweep of the tibia to their prey's approach. The use of visual inputs to adjust the motor pattern controlling forelimb movements shows that not all aspects of the strike are stereotyped and that sit-and-wait predators can produce behavioural flexibility.

1. Introduction

Many predators hunt and capture moving prey that are, in some cases, actively attempting to avoid or escape from them [1]. Catching such prey requires that predators show considerable behavioural flexibility, which is often associated with higher cognitive abilities and relatively large-brained vertebrates [2]. Yet insects with relatively small brains can use simple behavioural rules to produce effective attack strategies that may seem superficially complex [3–6]. The majority of studies of insect predators have focussed on the flexibility of those that chase prey [6–10] rather than those that 'sit-and-wait' for prey. If such sit-and-wait predators, which may have just a single opportunity to capture prey, can adjust their hunting behaviour, then they may improve their success.

Although capable of chasing prey when hungry [11–13], praying mantids are primarily sit-and-wait predators employing crypsis to catch a variety of animals, including some vertebrates [14–17]. Mantids are visual predators, whose visual system shows numerous adaptations for prey capture including regions of high spatial acuity and binocular distance estimation [18–21]. Similarly, the mantid's forelimbs are highly adapted for prey capture, featuring movable and immovable spines on the femur and tibia, which facilitate prey capture both mechanically and behaviourally [22–24]. The raptorial strike of praying mantids can be divided into two behavioural phases, the approach and the sweep, and it has been studied in terms of both kinematics and mechanics [25–28]. The strike is often characterised as stereotypical but both phases of the strike are variable in duration, the approach being more variable than the sweep [29]. Although the source of variability has not been identified in the approach, variability in the duration of the sweep has been linked to the distance between predator and prey. This suggests that praying mantids may be a valuable model in which to study behavioural flexibility in relatively small-brained, sit-and-wait predators. Here we study the behavioural flexibility of the predatory strike of praying mantids in response to the speed at which their prey are moving. We show that praying mantids adjust the speed and structure of their strike duration in relation to prey speed.

2. Materials and methods

(a) Animals

Madagascan marbled praying mantids (*Polyspilota aeruginosa*) [30] were purchased from a local supplier (BugzUK, Norwich, Norfolk, U.K.) and maintained in individual cages at the University of Sussex, U.K. They were fed with live crickets and maintained in a 12/12 hour light/dark cycle at room temperature (21-23°C).

(b) Animal preparation, stimulus presentation and videography

To record strikes, mantids were placed on a black 10 x 10 cm cardboard platform, fixed on a 26 x 26 cm raiseable metal plate, in the middle of a 75 x 60 x 60 cm white arena illuminated from overhead

(electronic supplementary materials, figure S1). A target attached to a transparent fluorocarbon wire with a diameter of 0.16 mm (Airflo Fishing, Sightfree G3) was moved at constant speeds of either 200, 330, or 730 mm/s (referred to hereafter as slow, medium or fast prey speeds) near one end of the platform using a motor (MFA Como Drills, RE – 385). These speeds were representative of air speeds of flying insects such as fruit flies [31] and blowflies [32]. Targets were either 6 mm diameter dark plastic beads, blowflies or cricket nymphs ensuring the mantids were hungry whilst still being rewarded occasionally for hunting.

The animals were filmed through a circular aperture in the arena wall with a high-speed video camera (GC-PX100 JVC Ltd, Yokohama, Japan) at 200 frames per second. Analysis was performed offline using ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.). The attacks were divided in phases based on femoral and tibial movements (see Results). The number of frames in each phase was then used to calculate duration. Joint angles were measured on the limb closer to the camera, either directly with the inbuilt angle tool, or limb segments were tracked using the MTrackJ plugin [33] (electronic supplementary materials, figure S2).

(c) Statistical analysis

Statistical tests were implemented using R studio software, version 1.0.136, and R software, version 3.3.2 (R Core Team, 2013). The median (med) and interquartile range (IQR) were calculated using the "pastecs" and "stats" package. Assumptions of normality were tested using the Shapiro-Wilk test in the "pastecs" package. Assumptions of equality of variance were tested using the Levene's test in the "car" package. Correlations were tested using Pearson's *r* tests, implemented in the "Hmisc" package. Logistic regressions were implemented using generalised linear models in the "stats" package. Linear mixed-effects models were implemented using the "lmerTest" package. These models incorporated both random effects (individual, trial number) and fixed effects (phase category, phase duration, target speed, prey type). Effects that did not significantly improve our models (trial number, prey type) were not included in the final models (electronic supplementary material, table S1), except for 'individual', which was kept as a random effect due to experimental design. Interactions between fixed effects did not significantly improve any of our models. Models were compared using an analysis of variance (ANOVA), in the "stats" package. Variability was compared using an asymptotic test for equality of coefficient variation [34], in the "cvequality" package. For comparisons of non-normally distributed data with heterogeneous variance amongst the groups, we used a Friedman rank sum test [35] in the "stats" package. Post-hoc comparisons were made using two-tailed, paired-sample Wilcoxon signed-rank tests in the "stats" package, with Hommel's adjusted *p* values. Where appropriate, *p* values were adjusted to account for multiple testing in post-hoc tests.

3. Results

(a) Forelimb movements during a raptorial strike

Upon detecting a potential prey item, mantids prepared for a strike by raising their prothoracic tarsi from the ground and reducing the angles of thoraco-coxal, coxo-femoral and femoro-tibial (F-T) joints. After these preparatory movements, the animals performed raptorial strikes with paired forelimb movements (figure 1; electronic supplementary material, figure S3). The *approach* phase of the strike was characterised by tibial extension. Coxal protraction and femoral depression marked the end of *approach* and the onset of the *sweep* phase. During the *sweep*, the femur was depressed thrusting the distal forelimb forward towards the prey but the F-T joint angle initially showed no noticeable change. The tibia was subsequently flexed, terminating upon full flexion against the femur or against the target if one was caught. If the strike was successful, the forelimb was retracted and the prey brought towards the mouthparts.

(b) Variability in the duration of the *approach* but not the *sweep* phase during strikes

We measured the duration of each strike recorded, and the duration of its component phases [36]. The duration of raptorial strikes showed considerable variability (med=100, IQR=40 ms; n=96, N=8) due to variability in the duration of the approach phase, which was significantly more variable than that of the sweep phase (med=67.5, IQR=40 ms and med=35, IQR=6.3 ms, respectively; asymptotic test for equality of coefficient of variation, $D'AD$=72.7, p<0.001). This difference was particularly pronounced when comparing the movements of the tibia during strikes of varying durations, tibial extension being slower and more variable than tibial flexion (figure 2*a*). Strike duration was correlated significantly with approach but not sweep duration (Pearson correlation, r=0.99, p<0.001; r=-0.12, p=0.225, respectively; figure 2*b*).

Tibial extension during the approach phase lasted 65 ms (med, IQR=35), however, in 30% of strikes a distinct pause lasting 20 ms (med, IQR=25) occurred during which the tibia was stationary, interrupting the extension. Pauses were more frequent in the early stages of a strike. In contrast, during the sweep the thrust of the distal forelimb towards the prey and the subsequent tibial flexion to capture the prey were brief and showed little variability (med=10, IQR=5 ms and med=20, IQR=5 ms, respectively). Strike duration was determined by the duration of both tibial extension and the pauses (fixed effect tests, t(92.9)=37.4, p<0.001; t(91.1)=28.6, p<0.001, respectively) but not by thrusts and captures (fixed effect tests, t(92.9)=1.23, p=0.222; t(90.5)=1.43, p=0.157, respectively). Tibial extensions and pauses were positively correlated with one another, slower extensions being accompanied by longer pauses (Pearson correlation, r=0.5, p<0.001). Therefore, strike duration is primarily determined by the components (extensions and pauses) of the approach phase.

(c) Adjustment of *approach* duration to prey speed

One possible cause of the differences in strike duration is the speed at which the prey is approaching the mantid. We analysed the durations of strikes elicited by prey moving at three different speeds (see

Materials and Methods). Strike duration differed significantly with prey speed (Friedman's ANOVA $\chi^2(2)=20.12$, $p<0.001$, figure 2*c*); strikes to fast prey were faster than those to prey moving at medium speed (post-hoc test, $p=0.022$), and strikes to prey moving at medium speed were faster than those to slow prey ($p=0.002$).

The duration of the components of the approach phase differed significantly (fixed effect tests, $t(182)=18.5$, $p<0.001$) but were also affected by the approach speed of the prey (fixed effect tests, $t(182)=5.46$, $p<0.001$). When attacking slow prey, tibial extension paused in 56% of the strikes, compared to 25% of the strikes in response to medium prey speed, and 9.4% in response to fast prey. This suggests that the structure of the behavioural sequence producing a strike is dependent upon the approach speed of the prey. Indeed, prey speed predicted the presence of a pause during tibial extension, slower speeds predicting a significantly greater probability of pausing (logistic regression, $\chi^2(1)=15.7$ $p<0.001$). Our model shows that the probability of pause occurrence, *P(pause)*, depends on prey speed, *v*: $P(pause)=1/(1+e^{-0.93+0.005v})$.

Prey speed also affected the probability of a successful strike (logistic regression, $\chi^2(1)=20.0$, $p<0.001$), the probability of success, *P(success)*, depending upon prey speed, *v*, in the following way: $P(success)=1/(1+e^{-1.82+0.012v})$. The presence or absence of a pause did not affect the probability of a strike being successful (ANOVA, $\chi^2(1) = 0.0185$, $p = 0.892$).

4. Discussion

Predators often show considerable flexibility during prey capture [37–39] but the raptorial strikes of 'sit-and-wait' predators are often characterised as ballistic and stereotyped [40–42]. We investigated whether sit-and-wait predators show behavioural flexibility and whether such flexibility is related to their prey's behaviour using praying mantids as a model. We focussed on the movements of the forelimb tibia during the strike, which executes the final sweep that will trap the prey between the tibia and femur. Our analysis shows that the mantid's raptorial strike is flexible both in speed and in structure, and that this flexibility depends in part upon the speed of the approaching prey.

Flexibility within the tibial movements of the strike is found in the slower approach phase, which is highly flexible in duration, whereas the faster sweep phase shows little variability and high stereotypy. In many cases, flexibility is also evident in the behavioural structure of the strike; a pause is incorporated into the motor pattern, interrupting the extension of the forelimb's tibia after it has begun. Furthermore, the duration of these pauses can be varied by individuals. This contradicts early reports of stereotypy in the strike, which reported that the strike was too fast to be modified and even suggested it might be ballistic [43–45]. However, a previous study also found that behavioural phases of the mantid's strike differ in their variability, the approach being more variable than the sweep [29].

At least part of this variability is related to the speed at which the prey approaches the waiting mantid; when prey approach slowly, the approach phase of the strike is slower and incorporates pauses,

whereas when prey approach quickly the approach is fast and pauses are absent. Such flexibility allows the mantid to adjust its motor programme to prey velocity, even after the strike has been initiated. This may be important when hunting small flying animals with erratic flight paths that can be difficult to predict. Indeed, for sit-and-wait predators like mantids that may have just one opportunity to capture prey it is important to match the timing of the strike to their prey's behaviour.

Strikes can be aborted after they have been initiated (electronic supplementary material, figure S4), providing further evidence of flexibility [46]. Why such strikes are abandoned is unclear but given the relationship between the strike and the prey's approach speed, aborting a strike may relate to the mantids' ability to capture prey. Indeed, all the abandoned strikes we observed occurred when the prey was approaching at high speed, suggesting that they may be aborted when prey is travelling too fast to be caught.

The need for flexibility may explain why no power amplification has been found in the forelimb of praying mantids [25]. Indeed, the extension and flexion of the forelimb tibia are under direct muscular control (RS and JEN, 2016, unpublished observation). Consequently, mantids' flexibility in the approach phase of their strike is likely due to the direct muscular control. This would allow mantids to detect approaching prey and prepare the forelimb for the strike early, adjusting the approach phase to time the final rapid sweep phase of the strike. It is possible that mantids determine the duration of the tibial extension (approach phase) prior to initiating the strike, based on the approach velocity of their target. However, pauses during tibial extension and abandonment of the strike once initiated suggest such feedforward control of flexibility is unlikely. Instead, it seems more likely that mantids adjust their raptorial strike through visual inputs allowing them to determine prey speed, among other possible variables. In contrast, mantis shrimps use power-amplified appendages to strike prey [47]. The movements of the mantis shrimp's raptorial appendage joints during the strike are flexible due to feedforward motor commands [48,49], contrary to praying mantids.

Both desert locusts and horse-head grasshoppers use visual inputs to target the movements of their forelimbs [50–53]. In locusts, once these visually-targeted forelimb movements are initiated, they cannot be terminated and redirected until after the target has been missed [50]. Our evidence shows that mantids can adjust the timing of their strike motor pattern to match prey speed even after the strike has initiated. This suggests that, in terms of behavioural flexibility, the mantid strike exceeds that of the visually targeted forelimb movements of locusts. In horse-head grasshoppers, reaches are highly flexible and the forelimb movements adapted to the specific locations of targets within their frontal visual field [51]. However, it is unclear whether the mantid strike is so flexible in terms of spatial accuracy.

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Ethical statement. This work complied with relevant regulations and laws of the United Kingdom, where the work was conducted.

Data accessibility. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.59zw3r244 [36].

Authors' contributions. S.R. and J.E.N. designed the experiments/analysis. S.R. performed the experiments/analysis. Both authors equally contributed to the manuscript and approve of its final version. Both authors are accountable for all aspects of this work.

Competing interests. We declare we have no competing interests.

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Figures

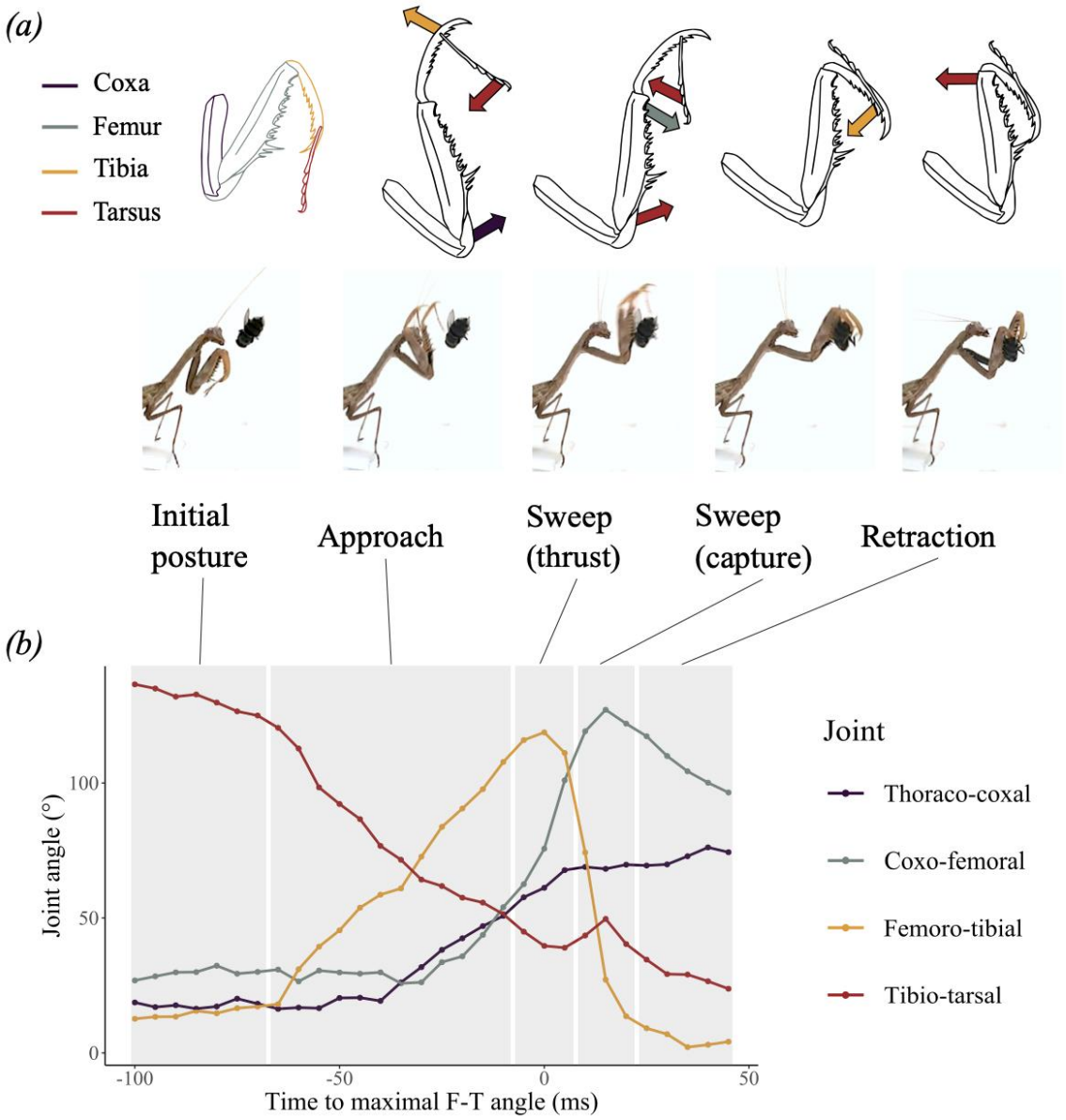

Figure 1. The predatory strike of *P. aeruginosa*. (*a*) The sequence of prothoracic limb movements during a strike. The main phases of the strike (*approach, thrust, capture, retraction*) are indicated. (*b*) The change in angles between the different prothoracic joints during a typical strike.

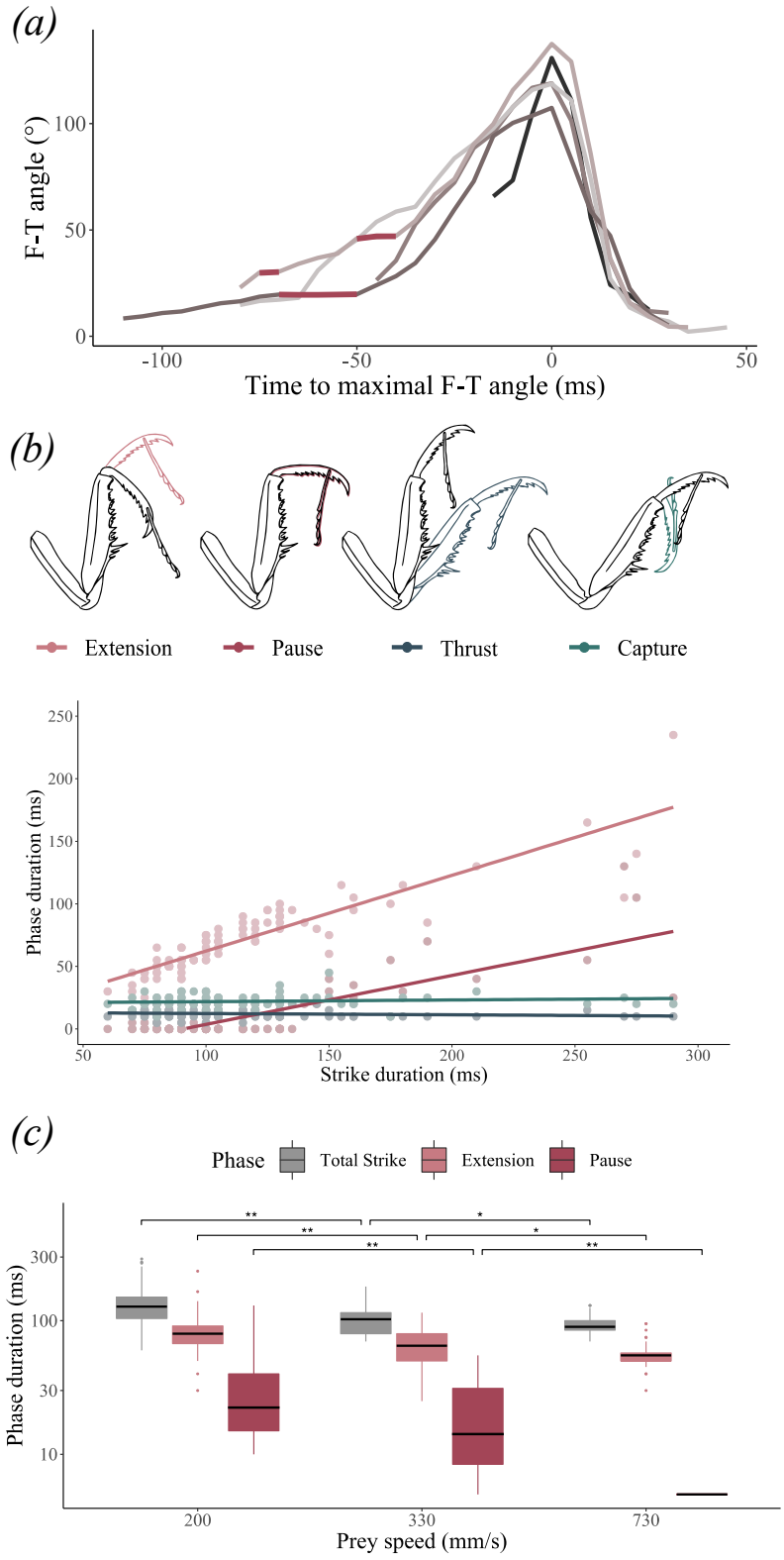

Figure 2. Strikes duration is adjusted to prey speed. (*a*) The F-T joint angles of five strikes superimposed upon one another. The pauses in two strikes are highlighted in dark red. (*b*) *Above*. Schematic of the movements of the mantid forelimb. *Below*. Strike duration is correlated with the duration of tibial extension and pauses. (*c*) Strike duration and the duration of tibial extensions and pauses decreases with increasing prey speed. Phase durations are plotted on a log scale. Significance values: * = $p < 0.05$, ** = $p < 0.01$, n.s. = $p > 0.05$.